

Research Article

Insights from paedomorphic newts in introduced populations

Mathieu Denoël¹ 

¹ Laboratory of Ecology and Conservation of Amphibians (LECA), Freshwater and Oceanic Unit of Research (FOCUS), University of Liège, 22 Quai van Beneden, 4020 Liège, Belgium

Corresponding author: Mathieu Denoël (Mathieu.Denoel@uliege.be)

Abstract

Facultative paedomorphosis is a widespread polyphenism in newts and salamanders, but it is declining due to the introduction of non-native species. Conversely, caudates have often been introduced outside their range and could be good models to improve our understanding of the factors that facilitate the expression of metamorphosis versus paedomorphosis. In particular, the alpine newt is a common amphibian species that has been introduced into many countries and whose many native paedomorphic populations have become extinct. By surveying ponds where metamorphic alpine newts were introduced in France over eight years, this study aimed to show what we can learn from such introduced populations by highlighting key life history traits of both phenotypes and a co-existing native species, the palmate newt, that can also express paedomorphosis. Although paedomorphosis is rare outside of the main European hotspots, paedomorphs were repeatedly found in the introduced population, including in a pond where they were dispersing. Interestingly, the relative frequencies of paedomorphs in the adult population of both species were low and match those of the paedomorphs of the native palmate newts over the years. This resulted in a complex size-structured newt community. Taken together, these results allow the discussion of alternative scenarios for the origin of aliens and possible reasons for the presence of paedomorphs in such populations. Ultimately, they call for reporting such developmental variants in the introduced populations of newts and salamanders and tracing the origin of the introductions to infer on genetic and environmental causes.

Key words: Alpine newt, biological introductions, eco-evo-devo, *Ichthyosaura alpestris*, invasive alien species, metamorphosis, *Mesotriton alpestris*, paedomorphosis



Academic editor:

Tammy Robinson-Smythe

Received: 5 March 2025

Accepted: 27 May 2025

Published: 27 June 2025

Citation: Denoël M (2025) Insights from paedomorphic newts in introduced populations. NeoBiota 99: 249–263. <https://doi.org/10.3897/neobiota.99.152115>

Copyright: © Mathieu Denoël.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Paedomorphosis in newts and salamanders is a developmental process in which individuals do not (fully) metamorphose and, therefore, retain larval features such as gills in the adult stage (Gould 1977; Whiteman 1994) (Fig. 1). This process is widespread in caudate families, where it can be obligatory or facultative (Bonett et al. 2022). In salamandrids, ambystomatids and plethodontids and, to a lesser extent hynobiids, both developmental pathways – paedomorphosis and metamorphosis – can be expressed within the same species and in the same habitats (Breuil 1992; Shaffer and Voss 1996; Takahashi et al. 2011; Bonett et al. 2014b; Okamiya et al. 2021). They are, therefore, good models for understanding the evolutionary ecology of both processes.

The prevalence of paedomorphosis is often higher in restricted parts of species' ranges (Denoël et al. 2001; Emel and Bonett 2011; Bonett et al. 2014a). For example, the alpine newt (*Ichthyosaura alpestris* or *Mesotriton alpestris*; nomenclature



Figure 1. Alien paedomorphic alpine newts from a population in southern France (Bagnelades pond, 13 May 2006): male with conspicuous secondary sexual traits (A) and female with unusual marbled colouration (B). The emergence of paedomorphosis outside its native range may help us to understand this rare developmental process. Photos by M. Denoël.

currently under debate) has the highest number of paedomorphic populations in southern Europe: from the south-western tip of the French Alps to the Italian and Balkan Peninsulas (Denoël et al. 2001). Within their distribution, they occupy a wide range of habitats, from lowland ponds to high mountain lakes (Denoël et al. 2001). Multiple environmental variables promote facultative paedomorphosis in newts and salamanders, such as the absence of fish and deep water (Denoël and Ficetola 2014; Denoël et al. 2019). As a facultative process in many species, paedomorphs retain the ability to metamorphose at the adult stage when water quality deteriorates (Semlitsch 1987; Denoël et al. 2007) (Fig. 1; Suppl. material 1). This could then explain the temporary presence of paedomorphs in apparently unfavourable waterbodies, such as those that can dry out in occasional years.

Despite the known effects of some global drivers, such as climate (Bonett et al. 2014a; Lyons and Arbuckle 2024), the reasons for the local expression of paedomorphosis remain poorly understood. There is evidence for genetic variation amongst populations in their probability of expressing paedomorphosis (Semlitsch et al. 1990), with a genetic threshold mechanism for the process, such as illustrated in ambystomatids (Semlitsch and Wilbur 1989). This means that not all populations are able to express paedomorphosis and that some may lose this ability (Bonett et al. 2014a). The dependence on environmental variables (Denoël and Ficetola 2014) also suggests that genotypes capable of expressing paedomorphosis only express it under certain conditions. From this perspective, determining the proportion of paedomorphs in adult populations can help to understand the relative success of the two morphs in different habitats (Denoël and Ficetola 2014; Kirk et al. 2023).

Fish introductions have been disastrous for paedomorphs in several species of newts and salamanders (Denoël and Winandy 2015; Davis et al. 2017; Denoël et al. 2019). For example, paedomorphic alpine newts disappeared from their main populations in the Alps and in the Montenegrin hotspots (Denoël et al. 2019; Denoël et al. 2023). Such extinctions raise awareness of the global persistence of the process and the need to find situations where paedomorphs can persist despite the risk of disturbance (Denoël and Winandy 2015).

Under experimental conditions, paedomorphs of facultatively paedomorphic species, such as alpine newts, typically metamorphose rapidly (Denoël 2003), suggesting that the process may not be expressed when paedomorphs are released into new habitats. Biological introductions can, therefore, be good models for understanding the adaptability of organisms to new environmental conditions (Shine 2012; Vimercati et al. 2018; Mühlenhaupt et al. 2021). As environmental and genetic additive and interactive processes are likely to be affected in introduced populations, this also provides an opportunity to study metamorphic versus paedomorphic processes. European newts have been introduced to various locations, from which they have sometimes settled and even dispersed (Lever 2003; Dubey et al. 2019). The alpine newt is a colourful, small highly aquatic amphibian species, with many subspecies described, that adapts well to aquarium and has, therefore, been highly prized by captive breeders (Sotiropoulos et al. 2007; Staniszewski 2011; Schultschik 2018). It has, therefore, been by far the most translocated newt species in the world, mainly as an ornamental species or when private owners or researchers could no longer keep them in captivity (Arntzen et al. 2016; Ball et al. 2023), with introductions into several European countries: the United Kingdom (Allain and Lynn 2021; Ball et al. 2023; Cathrine 2024), Spain (Bosch et al. 2015; Palomar et al. 2017), the Netherlands (Robbemont et al. 2023), France

(Denoël 2005; Geniez and Cheylan 2012), Ireland (Meehan 2013), Italy (Novarini and Tagliapietra 2020), Bulgaria (Naumov and Langourov 2009), Denmark (Bringsøe 2018), Finland (Lappalainen et al. 2024) and probably Poland (Jakóbiak et al. 2019), but also as far as New Zealand (Bell 2016).

The main aim of this study was to show what we can learn from the expression of paedomorphosis in populations where metamorphs were originally introduced and in situations where paedomorphs of another species are also documented (Denoël 2005, 2007). Specifically, I aimed to determine: (1) whether the emergence of paedomorphosis is a transient phenomenon or a persistent life-history trait; (2) whether paedomorphosis is similarly expressed in the co-existing native palmate newt (*Lissotriton helveticus*) and the alien alpine newt across surveys; (3) whether paedomorphosis is present in the ponds to which the species has dispersed and (4) whether body size variation follows a similar differentiation amongst morphs in the alien and native species. More broadly, this study aimed to show how these natural history observations could provide clues to improve our understanding of the ecology of facultative paedomorphosis and, thus, provide perspectives for new research.

Materials and methods

Surveys took place mainly at the Bagnelades Pond on the Larzac Plateau (Municipality of Le Cros, Hérault, France; 43.85°N, 3.37°E (DD); 735 m a.s.l.; Suppl. material 2) once a year in May (i.e. at the peak of the breeding season) for eight years in the period 2002–2014. The newts are long-term breeders, spending several months in the water in Larzac (Denoël 2005). The alpine newt is the only introduced newt in Larzac, while the palmate newt and the marbled newt (*Triturus cristatus*) are both native (Denoël 2007; Geniez and Cheylan 2012; Denoël and Ficetola 2014). Bagnelades Pond is an unpaved natural pond, without fish or crayfish, surrounded by agricultural land (crops). The nearby ponds where the metamorphic alpine newt dispersed were also surveyed for the presence of paedomorphs (Bergerie de l'Hôpital 43.86°N, 3.37°E (DD) and Le Cros Farm 43.86°N, 3.36°E (DD), two man-made fishless agricultural ponds, located 1.5 and 1.7 km from Bagnelades Pond, respectively; Suppl. material 2) (Denoël 2005). More broadly, most Larzac ponds were surveyed as part of a research on palmate newts (Denoël and Ficetola 2015).

The survey protocol consisted of making dip-netting in all areas of the ponds (see, for example, Denoël and Ficetola (2014)). Newts were handled with wet disposable gloves and all materials were washed, disinfected, rinsed and dried after sampling the ponds. For each survey, the proportion of paedomorphs in the adult population was recorded for each species (minimum number of newts sampled per species and per survey: 29). This relative metric has the advantage of being independent of catching effort (Denoël and Ficetola 2014). Maturity was based on the presence of a developed cloaca in both sexes (Denoël 2017). An adult individual was considered a paedomorph if its gill slits were open (Denoël 2017) and in all cases paedomorphs also had external gills. Finally, the snout-vent length of newts (i.e. from the tip of the nose to the end of the cloaca) was measured with a ruler. All identifications and measurements were made by the same person to avoid observer effects. A paired *t*-test was used to compare newt proportions, a *t*-test to test Pearson's correlation and a linear model to test for a species, sex and morph effect on body size. All statistical tests were run in R.

Results

Paedomorphic alpine newts were found in five of the eight surveys at Bagnelades Pond, with the first finding in 2002 (Fig. 1). They represented only a small proportion of the adult population (mean \pm SE = $2 \pm 1\%$; max: 6%; Fig. 2). Paedomorphic palmate newts (*Lissotriton helveticus*) were also less abundant than their metamorphic counterparts, being present in seven of the eight surveys (mean \pm SE = $7 \pm 2\%$; max: 17%). These proportions differed significantly (paired t_7 -test = -3.1042, $P = 0.017$). There was a significant positive correlation between these proportions in the two species ($R = 0.80$, $t_6 = 3.291$, $P = 0.017$; Fig. 2). Some metamorphic marbled newts (*Triturus marmoratus*) were found in the pond.

There was a significant effect of species, sex and morph, as well as the interactions between species and sex and between species and morph on body size (Linear model, all $P < 0.001$; Fig. 3; Suppl. material 3). Alpine newts, metamorphs and females were, respectively, larger than palmate newts, paedomorphs and males.

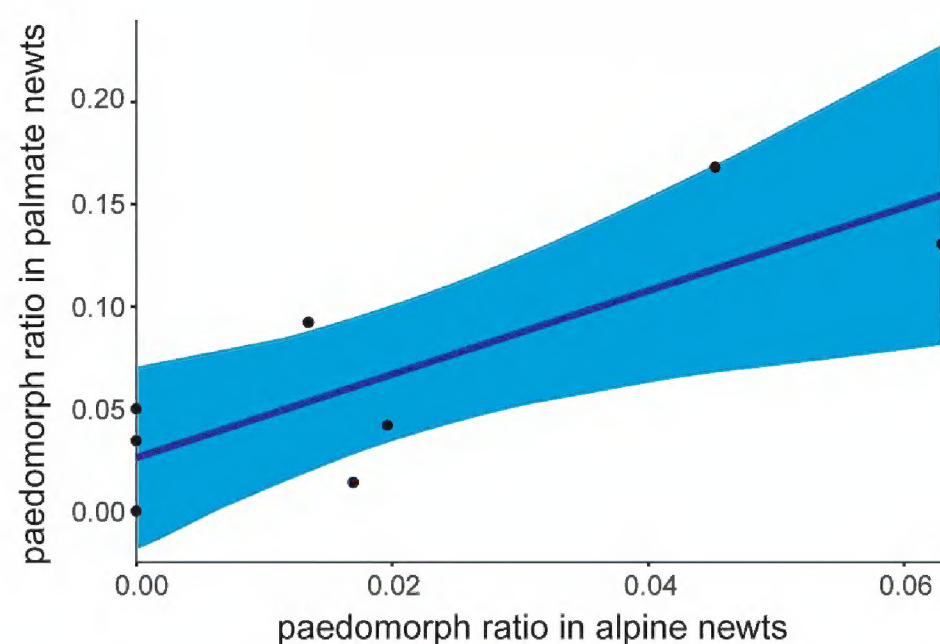


Figure 2. Proportion of paedomorphs in the adult populations of alien alpine and native palmate newts: correlative pattern between surveys in a population of southern France (linear regression and 95% confidence interval).

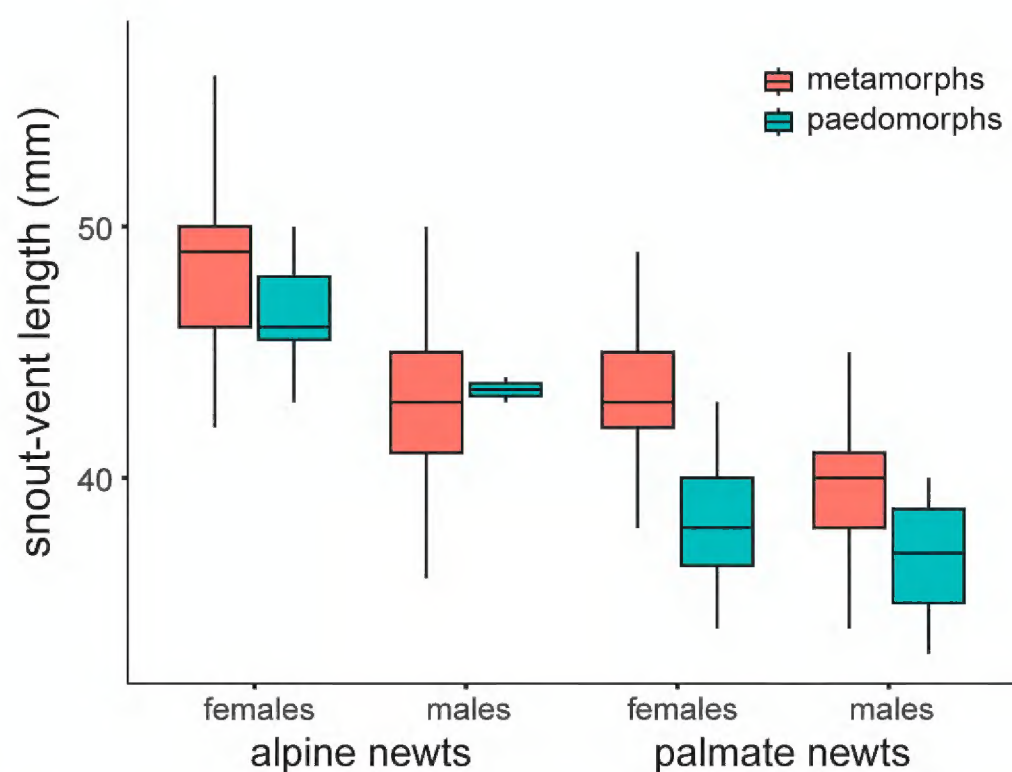


Figure 3. Size structure in paedomorphic and metamorphic alien alpine and native palmate newts in a southern French population. Box plots: median, quartiles and min-max no further than 1.5 interquartile range.

The interaction terms showed that paedomorphs were proportionally smaller in palmate newts than in alpine newts compared to metamorphs.

Alpine newts dispersed to Bergerie de l'Hôpital and Le Cros Farm ponds (first observations in 2003 and 2007, respectively), but only settled in the former. A single metamorphic alpine newt was also found in the drinking trough in front of Le Cros Farm Pond in 2005. In Bergerie de l'Hôpital Pond, both species expressed paedomorphosis, but paedomorphs were only found in two out of eight surveys. The low number of alpine newts makes it impossible to calculate morph ratios in this pond. Metamorphic marbled newts were also present in the two ponds.

Discussion

An important question for understanding the presence of paedomorphs is the origin of the introduced newts. Previous genetic analyses, using mtDNA and taking advantages of previous barcoding in Europe (Sotiropoulos et al. 2007; Recuero et al. 2014), showed the presence of two haplotypes attributed to the main lineage (subspecies *alpestris*) in the introduced Larzac population, one close to a wide range from France to Hungary (lineage C3) and the other not matching known populations, being 10 mutational steps from the main lineage and 14 from the Iberian lineage (subspecies *cyreni*). Although unlikely, this could have suggested a possible relict origin (Arntzen et al. 2016; but see Robbemont et al. (2023) for assignments in the main lineage). This hypothesis of a native remnant is, in fact, ruled out by local records of multiple introductions of metamorphic alpine newts into Larzac after being kept in aquariums in a nearby laboratory (J. Gabrion, pers. comm.). These observations are corroborated by J. Gabrion, who worked in the same laboratory for her Ph.D. on paedomorphosis in palmate newts (Gabrion 1976). The experimental research using alpine newt eggs was presented in several papers published in the 1960s and 1970s (Sentein 1966, 1970). Since alpine newts were collected, at least in part, in the French and/or Swiss Alps during vacation trips, Larzac was probably chosen as a convenient release site because of its proximity to the laboratory (J. Gabrion, pers. comm.) and because palmate newts were also being collected there at the same time period for similar research purposes (Sentein 1964, 1975). The alpine newts found in Bagnelades Pond are morphologically different from those of the only large French population of paedomorphs, located in the southern French Alps (Denoël 2017; pers. obs.) (Fig. 1; Suppl. material 1). The most likely explanation is that introduced newts came from areas without paedomorphs. In these areas, newts typically do not have the potential to express paedomorphosis as they almost never express this process across thousands of populations (Denoël et al. 2023). To address the issue of origin, future studies should use genome-wide molecular analyses (e.g. RADSeq) and have a more detailed understanding of the native distribution of the different haplotypes (Robbemont et al. 2023; Hester et al. 2025), provided they are not currently extinct (Denoël et al. 2019).

The fact that paedomorphs have been regularly found in Bagnelades Pond for more than 10 years, as well as in a nearby pond, shows that this is not an anecdotal phenomenon. Two scenarios can be proposed. First, as the newts were moved to new habitats, new gene-environment interactions may have occurred, leading to developmental perturbations. Life history transitions in contemporary species are mostly known from paedomorphosis to metamorphosis (Davis et al. 2017; Denoël et al. 2019). Similar to recent observations of new habitat use by obligate paedomorphs (Manenti et al. 2024), new research on the emergence of paedomorphosis from populations of meta-

morphs may provide new clues to the drivers involved. Second, the fact that individuals from different populations are likely mixed (J. Gabrion, pers. comm) which is also supported by the presence of two distant haplotypes (Arntzen et al. 2016) involves crosses that may have altered developmental programmes. Indeed, previous experimental crosses between paedomorphic and metamorphic taxa have improved our understanding of the molecular mechanisms of developmental pathways. They showed the presence of quantitative trait loci (QTL) of paedomorphosis versus metamorphosis (Voss and Shaffer 1997) and the role of artificial selection on altering such QTL (Voss and Shaffer 2000). In addition, in-depth transcriptomic studies (Tribondeau et al. 2021) would help to understand the molecular pathways involved.

Interestingly, alpine newts are not the only newt species expressing paedomorphosis in the two ponds: palmate newts also expressed paedomorphosis. In palmate newts, this is a typical alternative life history in the study area (Gabrion et al. 1977; Denoël 2007). It can be assumed that some local conditions might favour paedomorphosis in those taxa that are able to switch to such an alternative developmental pathway. From a broader perspective, facultative paedomorphosis may be a step towards either obligate metamorphosis or paedomorphosis (Everson et al. 2021; Lyons and Arbuckle 2024). Therefore, reporting and understanding the temporal dynamics of these two processes would help to understand their potential fixation or disappearance. Standardised repeated surveys, including capture-mark-recapture surveys, would therefore provide valuable insights into the local determinants of the alternative processes (Bruni et al. 2018; Lackey et al. 2019; Sandoval and Anderson 2025). The results from Bagnelades Pond show that the proportion of paedomorphs in the population was higher for both species in the same years. This supports the view that the same drivers may influence the evolutionary trajectories of species that evolved in different geographic areas and now co-exist as a result of human-mediated translocation.

Marbled newts, on the other hand, did not develop into paedomorphs in the study area, including the alpine newt ponds. This shows that local conditions alone do not prevent metamorphosis, which may also rule out strictly mechanistic approaches to paedomorphosis (Sprules 1974), as previously proposed by Breuil (1992). Furthermore, most of the palmate and alpine newt larvae in Bagnelades Pond metamorphose, suggesting that metamorphosis is the most selected trait in this population. Although paedomorphs are found in many palmate newt populations in Larzac (Denoël 2007), the area where alpine newts were introduced is on the edge of the hotspot of paedomorphosis in the palmate newt (Denoël and Ficetola 2015). Although densities are not known in the ponds studied, it is possible that this factor may also have influenced developmental pathways (Semlitsch 1987; Sandoval and Anderson 2025). In particular, as a size-structured social context can influence the expression of paedomorphosis (Moore et al. 2020), the presence of paedomorphs of two species and metamorphs of three species may lead to a complex biotic background.

Of the dozens of introduced populations of alpine newts in Europe and as far away as New Zealand, paedomorphs have been observed in two other ponds in Hampstead, close to London in the UK (Atkins & Hester, pers. comm.). The alpine newt paedomorphs photographed by Atkins in 2012 and coming from a disused swimming pool have phenotypic characteristics (dotted throat) typical of the subspecies *I. a. apuana* (*M. a. apuanus*), which is known to host many populations of paedomorphs (Andreone and Dore 1991; Denoël et al. 2001; Chiocchio et al. 2017). Alpine newt populations of the United Kingdom could be a good model due to the high number of invaded ponds in the country (Allain and Lynn

2021). Several approaches, including ddRAD-sequencing have already been used to depict the genetic diversity of introduced alpine newts across populations and to track their invasion (Ball et al. 2023; Hester et al. 2025). This may provide an opportunity to fine-tune analyses on populations with paedomorphosis, while awaiting new sampling to potentially find additional paedomorphic populations.

Another interesting pattern that may emerge from the study of introduced versus native paedomorphs and metamorphs is whether the same environment is associated with a similar shift in somatic and gonadal development (Ryan and Semlitsch 1998). Indeed, paedomorphosis could be the result of different developmental processes (Denoël and Joly 2000), such as progenesis and neoteny *sensu* Gould (1977) and give rise to different size patterns (Denoël et al. 2009). In progenesis, paedomorphs mature earlier and have a smaller size than metamorphs, whereas in neoteny, both morphs typically have similar age and size structures (see also Kalezić et al. (1996)). In Bagnelades Pond, paedomorphs of both species had, globally, a smaller size than metamorphs. This may suggest similar developmental patterns, but both species and sex-specific effects suggest variation. In addition to a well-developed cloaca, paedomorphic alpine newt males expressed other secondary sexual traits such as nuptial colouration, which can be as well developed in paedomorphs as in metamorphs (Fig. 1; Suppl. material 1). Some paedomorphic females also exhibited an unusually conspicuous marbled colouration (Fig. 1). Research on the relationships between paedomorphosis and colouration is awaited.

Finally, the findings on metamorphic and paedomorphic alien newts require an assessment of the risks they may pose to native amphibian populations. Paedomorphic alpine newts cannot disperse on land (but see Denoël 2003 for short movements), but metamorphs can. The degree of invasion of non-native populations of alpine newts varies between geographical areas, but is lower than that of non-native anurans in Europe (Fouquet and Measey 2006; Ball et al. 2023; Denoël and Dufresnes 2025). In Larzac, despite dozens of ponds surveyed in the surrounding area, alien alpine newts were only found in the three closest waterbodies (Denoël 2005; this study), suggesting low landscape penetration over the five decades of their presence. In contrast, introduced marsh frogs invaded most of the ponds in the same geographical area (Denoël et al. 2022). Ecological modelling in the UK has suggested that the success of different alpine newt lineages in invaded areas may vary depending on local climatic conditions (North et al. 2025). The presence of other newt species may also limit the success of the invader. On the other hand, because newt populations are size-structured (see Fig. 3), the introduction of paedomorphic and metamorphic alpine newts can result in complex competitive and predatory pressures on local communities (Joly and Giacoma 1992; Fasola 1993). For example, both paedomorphic and metamorphic alpine newts (especially females) consume newt eggs, but also feed opportunistically on most aquatic invertebrates (Denoël and Andreone 2003). It is still unlikely that alien newts will replace local native populations as they co-exist in the native range of the alpine newt (Griffiths 1996). However, alpine newts may be asymptomatic carriers and, therefore, potential vectors of diseases, particularly those that threaten caudates, such as chytridiomycosis caused by the chytrid fungus *Batrachochytrium salamandrivorans* “BSal” (Allain and Duffus 2019; Beninde et al. 2021; Castro Monzon et al. 2022). In a previous study, chytrids (*Batrachochytrium dendrobatidis* “Bd”) were not detected in palmate newts from the main pond studied, Bagnelades (González-Hernández et al. 2010) and no abnormal mortality events were detected in amphibians from ponds invaded by alpine newts in

Larzac (M. Denoël, pers. obs.). However, chytrids and other pathogens may pose a risk in other geographical areas where alpine newts were introduced, as Bd, Bsal and ranavirus have been found in captive-bred and released non-native alpine newts in other populations (Bell 2016; Martinez-Silvestre et al. 2017; M. Denoël, pers. obs.).

Conclusions

The presence of paedomorphs in introduced populations has raised a plethora of questions and, thus, some new perspectives for unravelling the drivers of alternative developmental pathways and the consequences of polyphenic alien species (i.e. capable of both metamorphosis and paedomorphosis). On the one hand, they show the interest of studying invaders to understand the natural history and evolutionary ecology of newts and other organisms. On the other hand, they highlight important research perspectives and the need for more extensive surveys across environments in several dimorphic species to unravel the mysteries of paedomorphosis.

Acknowledgements

I thank C. Bary, N. Belleuvre, M. Bichot, C. Houdoin, F. Hourlay and A. Lagaly for their help during the fieldwork, the Préfecture of Hérault and the Direction régionale de l'environnement, de l'aménagement et du logement du Languedoc Roussillon for providing the study permits, Le Cros Farm (D. Desfrères) and municipality of Le Cros (A. Viala) for allowing access to the ponds, W. Atkins, J. Gabrion and R. Hester for sharing personal observations and R.A. Griffiths and an anonymous reviewer for their constructive comments on the manuscript. M. Denoël is a Research Director of the Fonds de la Recherche Scientifique – FNRS.

Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

This is a field observational study. All newts were handled with care and manipulations followed ethical standards approved by the Ethical Committee of the University of Liège.

Funding

This research was funded by F.R.S.-FNRS grants 1.5.011.03, 1.5.120.04, J.008.13 and J.0044.23

Author contributions

The author solely contributed to this work.

Author ORCIDs

Mathieu Denoël  <https://orcid.org/0000-0002-3586-8323>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information. Datasets generated during the current study are available from the corresponding author on reasonable request.

References

- Allain SJ, Duffus AL (2019) Emerging infectious disease threats to European herpetofauna. *The Herpetological Journal* 29: 189–206. <https://doi.org/10.33256/hj29.4.189-206>
- Allain SJ, Lynn VJ (2021) Distribution of the alpine newt *Ichthyosaura alpestris* in Great Britain updated using social media. *Herpetological Bulletin* 158: 28–31. <https://doi.org/10.33256/hb158.2831>
- Andreone F, Dore B (1991) New data on paedomorphism in Italian populations of the Alpine newt, *Triturus alpestris* (Laurenti, 1768) (Caudata: Salamandridae). *Herpetozoa* (Wien) 4: 149–156.
- Arntzen JW, King TM, Denoël M, Martínez-Solano I, Wallis GP (2016) Provenance of *Ichthyosaura alpestris* (Caudata: Salamandridae) introductions to France and New Zealand assessed by mitochondrial DNA analysis. *The Herpetological Journal* 26: 49–56.
- Ball SE, Gupta M, Aldridge SJ, Allen BE, Faulkner SC, Oteo-García G, Griffiths RA, Hill P, Morris NJ, Stevens MCA, Wilkinson J, Garner TWJ (2023) Multiple introductions and human-aided dispersal of the UK's most widespread non-native amphibian. *Frontiers in Amphibian and Reptile Science* 1: 1215723. <https://doi.org/10.3389/famrs.2023.1215723>
- Bell BD (2016) A review of potential alpine newt (*Ichthyosaura alpestris*) impacts on native frogs in New Zealand. *Journal of the Royal Society of New Zealand* 46: 214–231. <https://doi.org/10.1080/03036758.2016.1216455>
- Beninde J, Keltsch F, Veith M, Hochkirch A, Wagner N (2021) Connectivity of Alpine newt populations (*Ichthyosaura alpestris*) exacerbates the risk of *Batrachochytrium salamandrivorans* outbreaks in European fire salamanders (*Salamandra salamandra*). *Conservation Genetics* 22: 653–659. <https://doi.org/10.1007/s10592-021-01377-8>
- Bonett RM, Steffen MA, Lambert SM, Wiens JJ, Chippindale PT (2014a) Evolution of paedomorphosis in plethodontid salamanders: Ecological correlates and re-evolution of metamorphosis. *Evolution* 68: 466–482. <https://doi.org/10.1111/evo.12274>
- Bonett RM, Steffen MA, Robison GA (2014b) Heterochrony repolarized: A phylogenetic analysis of developmental timing in plethodontid salamanders. *EvoDevo* 5: 27. <https://doi.org/10.1186/2041-9139-5-27>
- Bonett RM, Ledbetter NM, Hess AJ, Herrboldt MA, Denoël M (2022) Repeated ecological and life cycle transitions make salamanders an ideal model for evolution and development. *Developmental Dynamics* 251: 957–972. <https://doi.org/10.1002/dvdy.373>
- Bosch J, Palomar G, Vörös J (2015) El tritón alpino (*Mesotriton alpestris*) en el macizo de Peñalara (Madrid). *Boletín de la Asociación Herpetológica Española* 26: 9–12.
- Breuil M (1992) La néoténie dans le genre *Triturus*: Mythes et réalités. *Bulletin de la Société Herpétologique de France* 61: 11–44.
- Bringsøe H (2018) Bjergssalamander (*Ichthyosaura alpestris*) indført til Bernstorffsparken i det nordlige København Kan det forsvares at flytte bjergssalamandre? *Flora and Fauna* 124: 16–21.
- Bruni G, Tessa G, Angelini C (2018) Body size, age and population structure of *Triturus carnifex* (Urodela: Salamandridae) in the context of facultative paedomorphosis. *Acta Herpetologica* 13: 177–183. https://doi.org/10.13128/Acta_Herpetol-21972
- Castro Monzon F, Rödel M-O, Ruland F, Parra-Olea G, Jeschke JM (2022) *Batrachochytrium salamandrivorans*' Amphibian host species and invasion Range. *EcoHealth* 19: 475–486. <https://doi.org/10.1007/s10393-022-01620-9>
- Cathrine C (2024) Distribution of non-native terrestrial and freshwater amphibians and reptiles in Scotland. *Glasgow Naturalist* 28: 72–78. <https://doi.org/10.37208/tgn28225>
- Chiocchio A, Bisconti R, Zampiglia M, Nascetti G, Canestrelli D (2017) Quaternary history, population genetic structure and diversity of the cold-adapted Alpine newt *Ichthyosaura alpestris* in peninsular Italy. *Scientific Reports* 7: 2955. <https://doi.org/10.1038/s41598-017-03116-x>

- Davis CL, Miller DAW, Walls SC, Barichivich WJ, Riley J, Brown ME (2017) Life history plasticity does not confer resilience to environmental change in the mole salamander (*Ambystoma talpoideum*). *Oecologia* 183: 739–749. <https://doi.org/10.1007/s00442-017-3810-y>
- Denoël M (2003) How do paedomorphic newts cope with lake drying? *Ecography* 26: 405–410. <https://doi.org/10.1034/j.1600-0587.2003.03366.x>
- Denoël M (2005) Persistence et dispersion d’une population introduite de triton alpestre (*Triturus alpestris*) dans les causses du Larzac (sud de la France). *Revue d’Ecologie* 60: 139–148. <https://doi.org/10.3406/revec.2005.1252>
- Denoël M (2007) Priority areas of intraspecific diversity: Larzac, a global hotspot for facultative paedomorphosis in amphibians. *Animal Conservation* 10: 110–118. <https://doi.org/10.1111/j.1469-1795.2006.00081.x>
- Denoël M (2017) On the identification of paedomorphic and overwintering larval newts based on cloacal shape: Review and guidelines. *Current Zoology* 63: 165–173. <https://doi.org/10.1093/cz/zow054>
- Denoël M, Andreone F (2003) Trophic habits and aquatic microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) in a pond in central Italy. *Belgian Journal of Zoology* 133: 95–102. <https://doi.org/10.1643/CE-02-224R1>
- Denoël M, Dufresnes C (2025) The alien marsh frog cocktail: Distribution, causes and pathways of a global amphibian invasion. *Biological Conservation* 306: 111120. <https://doi.org/10.1016/j.biocon.2025.111120>
- Denoël M, Ficetola GF (2014) Heterochrony in a complex world: Disentangling environmental processes of facultative paedomorphosis in an amphibian. *Journal of Animal Ecology* 83: 606–615. <https://doi.org/10.1111/1365-2656.12173>
- Denoël M, Ficetola GF (2015) Using kernels and ecological niche modeling to delineate conservation areas in an endangered patch-breeding phenotype. *Ecological Applications* 25: 1922–1931. <https://doi.org/10.1890/14-1041.1>
- Denoël M, Joly P (2000) Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia: Caudata). *Proceedings of the Royal Society B, Biological Sciences* 267: 1481–1485. <https://doi.org/10.1098/rspb.2000.1168>
- Denoël M, Winandy L (2015) The importance of phenotype diversity in conservation: Resilience of palmate newt morphotypes after fish removal in Larzac ponds (France). *Biological Conservation* 192: 402–408. <https://doi.org/10.1016/j.biocon.2015.10.018>
- Denoël M, Duguet R, Džukić G, Kalezić ML, Mazzotti S (2001) Biogeography and ecology of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *Journal of Biogeography* 28: 1271–1280. <https://doi.org/10.1046/j.1365-2699.2001.00634.x>
- Denoël M, Lena JP, Joly P (2007) Morph switching in a dimorphic population of *Triturus alpestris* (Amphibia, Caudata). *Evolutionary Ecology* 21: 325–335. <https://doi.org/10.1007/s10682-006-9103-2>
- Denoël M, Ivanović A, Džukić G, Kalezić ML (2009) Sexual size dimorphism in the evolutionary context of facultative paedomorphosis: Insights from European newts. *BMC Evolutionary Biology* 9: 278. <https://doi.org/10.1186/1471-2148-9-278>
- Denoël M, Ficetola GF, Sillero N, Džukić G, Kalezić ML, Vukov TD, Muhović I, Ikoć V, Lejeune B (2019) Traditionally managed landscapes do not prevent amphibian decline and the extinction of paedomorphosis. *Ecological Monographs* 89: e01347. <https://doi.org/10.1002/ecm.1347>
- Denoël M, Duret C, Lorrain-Soligon L, Padilla P, Pavis J, Pille F, Tendron P, Ficetola G, Falaschi M (2022) High habitat invasibility unveils the invasiveness potential of water frogs. *Biological Invasions* 24: 3447–3459. <https://doi.org/10.1007/s10530-022-02849-9>
- Denoël M, Schmidt BR, Fonters R, Hansbauer G, Johanet A, Kühnis J, Poboljsaj K, Schweiger S, Sillero N (2023) Quantifying rarity of intraspecific diversity at multiple spatial scales by combining

- fine-grain citizen-based data across national boundaries. *Biological Conservation* 280: 109937. <https://doi.org/10.1016/j.biocon.2023.109937>
- Dubey S, Lavanchy G, Thiebaud J, Dufresnes C (2019) Herps without borders: A new newt case and a review of transalpine alien introductions in western Europe. *Amphibia-Reptilia* 40: 13–27. <https://doi.org/10.1163/15685381-20181028>
- Emel SL, Bonett RM (2011) Considering alternative life history modes and genetic divergence in conservation: A case study of the Oklahoma salamander. *Conservation Genetics* 12: 1243–1259. <https://doi.org/10.1007/s10592-011-0226-9>
- Everson KM, Gray LN, Jones AG, Lawrence NM, Foley ME, Sovacool KL, Kratovil JD, Hotaling S, Hime PM, Storfer A, Parra-Olea G, Percino-Daniel R, Aguilar-Miguel X, O'Neill EM, Zambrano L, Shaffer HB, Weisrock DW (2021) Geography is more important than life history in the recent diversification of the tiger salamander complex. *Proceedings of the National Academy of Sciences of the United States of America* 118: e2014719118. <https://doi.org/10.1073/pnas.2014719118>
- Fasola M (1993) Resource partitioning by three species of newts during their aquatic phase. *Ecography* 16: 73–81. <https://doi.org/10.1111/j.1600-0587.1993.tb00060.x>
- Fouquet A, Measey GJ (2006) Plotting the course of an African clawed frog invasion in Western France. *Animal Biology (Leiden, Netherlands)* 56: 95–102. <https://doi.org/10.1163/157075606775904722>
- Gabrion J (1976) La néoténie chez *Triturus helveticus* Raz. Etude morphofonctionnelle de la fonction thyroïdienne. PhD Thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France, 499 pp.
- Gabrion J, Sentein P, Gabrion C (1977) Les populations néoténiques de *Triturus helveticus* Raz. des Causses et du Bas-Languedoc. I. Répartition et caractéristiques. *La Terre et la Vie* 31: 489–506. <https://doi.org/10.3406/revec.1978.5028>
- Geniez P, Cheylan M (2012) Les amphibiens et les reptiles du Languedoc-Roussillon et régions limitrophes. Atlas biogéographique. Biotope and Museum National d'Histoire Naturelle, Mèze and Paris, 448 pp.
- González-Hernández M, Denoël M, Duffus AJL, Garner TWJ, Acevedo-Whitehouse K (2010) Dermocystid infection and associated skin lesions in free-living palmate newts (*Lissotriton helveticus*) from southern France. *Parasitology International* 59: 344–350. <https://doi.org/10.1016/j.parint.2010.04.006>
- Gould SJ (1977) Ontogeny and phylogeny. Harvard University Press, Cambridge, MA, 501 pp.
- Griffiths RA (1996) Newts and salamanders of Europe. T. & A. D. Poyser Natural History, London, 188 pp.
- Hester R, Labisko J, Wang J, Garner TWJ (2025) Invasion genomics of the alpine newt in Britain reveal a complex history of introductions and translocations. preprint Authorea: <https://doi.org/10.22541/au.173650524.41144486/v1>
- Jakóbić J, Janowski P, Błażuk J, Narczyński T, Pabijan M (2019) An Alpine newt (*Ichthyosaura alpestris*) population on the Baltic coast of Poland. *Herpetology Notes* 12: 923–930.
- Joly P, Giacoma C (1992) Limitation of similarity and feeding habits in three syntopic species of newts (*Triturus*, Amphibia). *Ecography* 15: 401–411. <https://doi.org/10.1111/j.1600-0587.1992.tb00050.x>
- Kalezić ML, Cvetković D, Djorović A, Džukić G (1996) Alternative life-history pathways: Paedomorphosis and adult fitness in European newts (*Triturus vulgaris* and *T. alpestris*). *Journal of Zoological Systematics and Evolutionary Research* 34: 1–7. <https://doi.org/10.1111/j.1439-0469.1996.tb00804.x>
- Kirk MA, Reider KE, Lackey ACR, Thomas SA, Whiteman HH (2023) The role of environmental variation in mediating fitness trade-offs for an amphibian polyphenism. *Journal of Animal Ecology* 92: 1815–1827. <https://doi.org/10.1111/1365-2656.13974>
- Lackey ACR, Moore MP, Doyle J, Gerlanc N, Hagan A, Geile M, Eden C, Whiteman HH (2019) Lifetime fitness, sex-specific life history, and the maintenance of a polyphenism. *American Naturalist* 194: 230–245. <https://doi.org/10.1086/704156>

- Lappalainen T, Di Minin E, Siljander M (2024) Mapping invasive alien species distributions in Finland using citizen science data. Master Thesis. Finland: University of Helsinki, 92 pp.
- Lever C (2003) Naturalised reptiles and amphibians of the world. Oxford University Press, New York, 318 pp. <https://doi.org/10.1093/oso/9780198507710.001.0001>
- Lyons TA, Arbuckle K (2024) The neoteny goldilocks zone: The evolution of neoteny in *Ambystoma*. Ecology and Evolution 14: e11240. <https://doi.org/10.1002/ece3.11240>
- Manenti R, Di Nicola MR, Zampieri V, Grassi G, Creanza T, Mauri E, Ficetola GF, Barzaghi B (2024) Wandering outside of the Styx: Surface activity of an iconic subterranean vertebrate, the olm (*Proteus anguinus*). Ecology 105: e4252. <https://doi.org/10.1002/ecy.4252>
- Martinez-Silvestre A, Montori A, Oromi N, Soler J, Marschang R (2017) Detection of a *Ranavirus* in introduced newts in Catalonia (NE Spain). Herpetology Notes 10: 23–26.
- Meehan ST (2013) IWT national smooth newt survey 2013 report. Irish Wildlife Trust, Dublin, Ireland: 16 pp.
- Moore MP, Pechmann JHK, Whiteman HH (2020) Relative size underlies alternative morph development in a salamander. Oecologia 193: 879–888. <https://doi.org/10.1007/s00442-020-04723-8>
- Mühlenhaupt M, Baxter-Gilbert J, Makhubo BG, Riley JL, Measey J (2021) Growing up in a new world: trait divergence between rural, urban, and invasive populations of an amphibian urban invader. NeoBiota 69: 103–132. <https://doi.org/10.3897/neobiota.69.67995>
- Naumov BY, Langourov MS (2009) The alpine newt (*Ichthyosaura alpestris*) in Vitosha mountain – an attempt for reintroduction [Алпийският тритон (*Ichthyosaura alpestris*) на Витоша – опит за реинтродукция]. In: Veltcheva I, Tsekov A (Eds) Anniversary scientific conference of ecology (2008) Proceedings. University Publishing House "Paisiy Hilendarski" [Университетско издателство „Пайсий Хилендарски“], Plovdiv, Bulgaria, 173–180.
- North AC, Sutton LJ, Brown JL, Garner TWJ, Billington RA, Wilkinson JW, Truebano M, Puschen-dorf R (2025) Predicting the invasiveness of alpine newts in the UK. Biological Invasions 27: 99. <https://doi.org/10.1007/s10530-025-03543-2>
- Novarini N, Tagliapietra A (2020) *Ichthyosaura alpestris* (Laurenti, 1768): An alien population in Lido di Venezia (NE Italy)(Amphibia, Urodela, Salamandridae). Bollettino del Museo di Storia Naturale di Venezia 71: 129–131.
- Okamiya H, Sugime R, Furusawa C, Inoue Y, Kishida O (2021) Paedomorphosis in the Ezo salamander (*Hynobius retardatus*) rediscovered after almost 90 years. Zoological Letters 7: 14. <https://doi.org/10.1186/s40851-021-00183-x>
- Palomar G, Vörös J, Bosch J (2017) Tracking the introduction history of *Ichthyosaura alpestris* in a protected area of Central Spain. Conservation Genetics 18: 867–876. <https://doi.org/10.1007/s10592-017-0934-x>
- Recuero E, Buckley D, García-París M, Arntzen JW, Cogălniceanu D, Martínez-Solano I (2014) Evolutionary history of *Ichthyosaura alpestris* (Caudata, Salamandridae) inferred from the combined analysis of nuclear and mitochondrial markers. Molecular Phylogenetics and Evolution 81: 207–220. <https://doi.org/10.1016/j.ympev.2014.09.014>
- Robbemont J, van Veldhuijzen S, Allain Steven JR, Ambu J, Boyle R, Canestrelli D, Cathasaigh ÉÓ, Cathrine C, Chiocchio A, Cogălniceanu D, Cvijanović M, Dufresnes C, Ennis C, Gandola R, Jablonski D, Julian A, Kranželić D, Lukanov S, Martínez-Solano I, Montgomery R, Naumov B, O'Neill M, North A, Pabijan M, Pushendorf R, Salvi D, Schmidt B, Sotiropoulos K, Stanescu F, Stanković D, Stapleton S, Šunje E, Szabolcs M, Vacheva E, Willis D, Zimić A, France J, Meilink Willem RM, Stark T, Struijk Richard PJH, Theodoropoulos A, de Visser Manon C, Wielstra B (2023) An extended mtDNA phylogeography for the alpine newt illuminates the provenance of introduced populations. Amphibia-Reptilia 44: 347–361. <https://doi.org/10.1163/15685381-bja10144>
- Ryan TJ, Semlitsch RD (1998) Intraspecific heterochrony and life history evolution: Decoupling somatic and sexual development in a facultatively paedomorphic salamander. Proceedings of

- the National Academy of Sciences of the United States of America 95: 5643–5648. <https://doi.org/10.1073/pnas.95.10.5643>
- Sandoval JL, Anderson TL (2025) Drivers of life history variation in a paedomorphic mole salamander. *Population Ecology* 67: 1–16. <https://doi.org/10.1002/1438-390X.12209>
- Schultschik G (2018) 3.6 *Ichthyosaura alpestris* (Laurenti, 1768)- Alpine newt. In: Grosse W-R (Ed.) *Mertensiella* 28 Threatened newts and salamanders - Captive care management Vol 2. Deutsche Gesellschaft für Herpetologie und Terrarienkunde, Mannheim, Germany, 62–73.
- Semlitsch RD (1987) Paedomorphosis in *Ambystoma talpoideum*: Effects of density, food, and pond drying. *Ecology* 68: 994–1002. <https://doi.org/10.2307/1938370>
- Semlitsch RD, Wilbur HM (1989) Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution; International Journal of Organic Evolution* 43: 105–112. <https://doi.org/10.1111/j.1558-5646.1989.tb04210.x>
- Semlitsch RD, Harris RN, Wilbur HM (1990) Paedomorphosis in *Ambystoma talpoideum*: Maintenance of population variation and alternative life-history pathways. *Evolution; International Journal of Organic Evolution* 44: 1604–1613. <https://doi.org/10.1111/j.1558-5646.1990.tb03849.x>
- Sentein P (1964) L'action de la vincalécoblastine sur la mitose chez *Triturus helveticus* Raz. *Chromosoma* 15: 416–456. <https://doi.org/10.1007/BF00368140>
- Sentein P (1966) L'action du dioxyde de sélénium sur des œufs d'amphibiens d'espèces résistantes. *Chromosoma* 19: 357–398. <https://doi.org/10.1007/BF00333045>
- Sentein P (1970) Action de la quinoline sur les mitoses de segmentation des oeufs d'urodèles: Le blocage de la centrosphère. *Chromosoma* 32: 97–134. <https://doi.org/10.1007/BF00334013>
- Sentein P (1975) Cytological action of pederin during the cleavage of the newt egg. *Caryologia* 28: 163–180. <https://doi.org/10.1080/00087114.1975.10796607>
- Shaffer HB, Voss SR (1996) Phylogenetic and mechanistic analysis of a developmentally integrated character complex: Alternate life history modes in ambystomatid salamanders. *American Zoologist* 36: 24–35. <https://doi.org/10.1093/icb/36.1.24>
- Shine R (2012) Invasive species as drivers of evolutionary change: Cane toads in tropical Australia. *Evolutionary Applications* 5: 107–116. <https://doi.org/10.1111/j.1752-4571.2011.00201.x>
- Sotiropoulos K, Eleftherakos K, Džukić G, Kalezić ML, Legakis A, Polymeni RM (2007) Phylogeny and biogeography of the alpine newt *Mesotriton alpestris* (Salamandridae, Caudata), inferred from mtDNA sequences. *Molecular Phylogenetics and Evolution* 45: 211–226. <https://doi.org/10.1016/j.ympev.2007.03.012>
- Sprules WG (1974) The adaptive significance of paedogenesis in North American species of *Ambystoma* (Amphibia: Caudata): an hypothesis. *Canadian Journal of Zoology* 52: 393–400. <https://doi.org/10.1139/z74-047>
- Staniszewski M (2011) *Salamanders and newts of Europe, North Africa and Western Asia*. Chimaira, Frankfurt am Main, Germany, 160 pp.
- Takahashi MK, Takahashi YY, Parris MJ (2011) Rapid change in life-cycle polyphenism across a subspecies boundary of the Eastern Newt, *Notophthalmus viridescens*. *Journal of Herpetology* 45: 379–384. <https://doi.org/10.1670/10-186.1>
- Tribondeau A, Sachs LM, Buisine N (2021) Are paedomorphs actual larvae? *Developmental Dynamics* 250: 779–787. <https://doi.org/10.1002/dvdy.304>
- Vimercati G, Davies SJ, Measey J (2018) Rapid adaptive response to a Mediterranean environment reduces phenotypic mismatch in a recent amphibian invader. *Journal of Experimental Biology* 221: jeb.174797. <https://doi.org/10.1242/jeb.174797>
- Voss SR, Shaffer HB (1997) Adaptive evolution via a major gene effect: Paedomorphosis in the Mexican axolotl. *Proceedings of the National Academy of Sciences of the United States of America* 94: 14185–14189. <https://doi.org/10.1073/pnas.94.25.14185>

Voss SR, Shaffer HB (2000) Evolutionary genetics of metamorphic failure using wild- caught vs. laboratory axolotls (*Ambystoma mexicanum*). *Molecular Ecology* 9: 1401–1407. <https://doi.org/10.1046/j.1365-294X.2000.01025.x>

Whiteman HH (1994) Evolution of facultative paedomorphosis in salamanders. *The Quarterly Review of Biology* 69: 205–221. <https://doi.org/10.1086/418540>

Supplementary material 1

Alien metamorphic alpine newts from a population in southern France (Bagnelades pond)

Author: Mathieu Denoël

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.99.152115.suppl1>

Supplementary material 2

Larzac ponds inhabited by alien alpine newts

Author: Mathieu Denoël

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.99.152115.suppl2>

Supplementary material 3

Results of a linear model on the effects species, sex, morph and their interactions on the body size (log snout-vent length) of newts in a southern French population inhabited by introduced alpine and native palmate newts

Author: Mathieu Denoël

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.99.152115.suppl3>